Universidade de Aveiro Departamento de Biologia
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Bárbara Cartagena da Silva Matos

As lontras-marinhas escolhem as suas presas de acordo com o valor nutricional?

Do sea otters forage according to prey's nutritional value?

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Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ecologia Aplicada, realizada sob a orientação científica da Doutora Heidi Christine Pearson, Professora Auxiliar da University of Alaska Southeast (Alasca, Estados Unidos da América) e do Doutor Carlos Manuel Martins Santos Fonseca, Professor Associado com Agregação do Departamento de Biologia da Universidade de Aveiro (Aveiro, Portugal).

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"*Two years he walks the earth. No phone, no pool, no pets, no cigarettes. Ultimate freedom. An extremist. An aesthetic voyager whose home is the road. Escaped from Atlanta. Thou shalt not return, 'cause "the West is the best." And now after two rambling years comes the final and greatest adventure. The climactic battle to kill the false being within and victoriously conclude the spiritual pilgrimage. Ten days and nights of freight trains and hitchhiking bring him to the Great White North. No longer to be poisoned by civilization he flees, and walks alone upon the land to become… lost in the wild.*"

Alexander Supertramp

o júri

presidente

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palavras-chave

Ecologia do comportamento de forrageio, ecologia da nutrição, mamíferos marinhos, carnívoros, dieta, sudeste do Alasca

resumo

A Teoria do Forrageio Ótimo propõe que o estímulo nutricional na escolha de presas e busca de alimento em carnívoros é o ganho energético. Em contraste, pesquisas recentes sugerem que os carnívoros selecionam presas que fornecem uma dieta com um equilíbrio específico de macronutrientes (gordura, proteína, hidratos de carbono), ao invés do maior conteúdo energético. Para este efeito, as escolhas de presas de lontras-marinhas (*Enhydra lutris*) que habitam Sitka Sound no sudeste do Alasca, foram estudadas durante os meses de maio a agosto de 2016. Os objetivos desta pesquisa foram: 1) descrever a dieta das lontras-marinhas em Sitka Sound; 2) descrever o valor nutricional das suas presas; 3) comparar diferenças na escolha de presas de acordo com o sexo; e 4) avaliar e comparar o valor nutricional das presas com as escolhas das lontras-marinhas. Os dados de observação foram coletados oportunisticamente, através de uma plataforma de oportunidade. As presas de lontras-marinhas foram capturadas em áreas arbitrárias de Sitka Sound, e analisadas quanto à sua percentagem em lípidos (teor de gordura) e calorias (densidade de energia). O consumo de presas foi significativamente diferente: as amêijoas foram as presas mais consumidas (68,6%), seguidos pelos ouriços-do-mar (14,3%), vieiras (5,7%), pepinos-do-mar (5,7%), caranguejos (2,9%) e estrelas-do-mar (2,9%). Além disso, os resultados revelaram uma significativa diversidade no conteúdo de gordura e densidade energética entre presas de lontra-marinha. O abalone registou maior teor de densidade energética, seguido pelas vieiras, enquanto que os ouriços-do-mar registaram maior teor em lípidos. A escolha de presas e a ingestão de nutrientes não diferiram significativamente entre machos e fêmeas, no entanto, os machos de lontras-marinhas consumiram mais moluscos do que as fêmeas, enquanto que as fêmeas consumiram mais ouriços-do-mar do que os machos. O trabalho sobre nutrição em carnívoros é preliminar, e estes resultados fornecem um ponto de partida para futuras pesquisas. As respostas a estas questões não só terão implicações significativas na gestão das populações de predadores e das comunidades ecológicas de que fazem parte, mas também acrescentarão informações importantes sobre a biologia de predadores que até agora foram negligenciadas. Além disso, os conflitos nas comunidades sobre os impactos que as lontras-marinhas têm na pesca comercial no sudeste do Alasca, não podem ser ignorados. Compreender as escolhas de presas de lontras-marinhas pode fornecer previsões de como a pesca pode ser afetada, de acordo com o crescimento da população de lontras nesta área, a fim de ajudar políticos, membros da comunidade e pescadores comerciais, a responder em conformidade.

keywords Foraging ecology, nutritional ecology, marine mammals, carnivores, diet, southeast Alaska

abstract

Foraging theory proposes that the nutritional driver of prey choice and foraging in carnivores is energy gain. In contrast, recent research suggests that carnivores select prey that provides a diet with a specific balance of macronutrients (fat, protein, carbohydrates), rather than the highest energy content. To this effect, the prey choices of sea otters (*Enhydra lutris*) inhabiting Sitka Sound, in southeast Alaska, were studied during the months of May-August of 2016. The goals of this research were to 1) describe sea otter's diet in Sitka Sound; 2) describe the nutritional value of sea otters' prey items; 3) compare differences in prey choice according to sex; and 4) evaluate and compare prey's nutritional value with sea otter's prey choices. Foraging observational data were collected opportunistically on a boat-based platform of opportunity. Sea otter's main prey were captured in arbitrary areas of Sitka Sound, and analyzed for percentage in lipids (fat content), and calories (energy density). Prey consumption was significantly different: clams were the most frequently consumed prey (68,6%), followed by sea urchins (14,3%), scallops (5,7%), sea cucumbers (5,7%), crabs (2,9%) and sea stars (2,9%). Also, the results revealed a significant diversity in content of fat and energy density between sea otter prey specimens. Abalone ranked first on content of energy density, followed by scallops, while sea urchins recorded the highest lipid content. Prey choice and nutrient intake were not significant different between male and female sea otters, nevertheless, males consumed more clams than females, while females consumed more sea urchins than males. The work on carnivore nutrition is preliminary, and these results provide a starting point for future work. Answers to such questions not only will have significant implications for managing predator populations and the ecological communities of which they are a part, but will also add important information on predator biology that has been neglected so far. Moreover, communities' conflicts over the impacts sea otters are having on commercial shellfisheries in southeast Alaska cannot be overlooked. Understanding sea otter's prey choices may provide information and predictions of how fisheries may be affected as the sea otter population grows in this area, in order to help decision makers, policy makers, community members, and commercial fishermen respond accordingly.

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1. INTRODUCTION

1.1 General background

1.1.1 Sea otter conservation: history, challenges and conflicts

The sea otter (*Enhydra lutris*, Linnaeus, 1758; Figure 1) is the second largest mustelid and the smallest marine mammal on the planet, representing one of 13 species of otters distributed worldwide, and also embodying the only member of the genus *Enhydra* (Kenyon 1969; Riedman & Estes 1990; Larson & Bodkin 2015). This genus has three recognized subspecies, based on skull measurements and mitochondrial DNA - the northern pacific *E. lutris kenyoni*, the southern pacific *E. lutris nereis*, and the pacific Asian *E. lutris lutris* (Wilson *et al*. 1991). Historically, sea otters occurred throughout the Pacific coasts of Mexico, United States, Russia and Japan; however, this species currently occupies approximately one half to two thirds of its former range (Barabash-Nikiforov 1947; Lensink 1962; Kenyon 1969; Bodkin 2015; see Appendix 1).

Fig. 1 Sea otter (*Enhydra lutris*). Photo by Bárbara Cartagena S. Matos

One of the challenges marine mammals face throughout their lives is insulation against heat loss to the cold aquatic environment in which they live, and while pinnipeds and cetaceans use blubber for that effect, sea otters depend entirely on their fur, and on their high metabolic rate that aids in

thermoregulation (Kenyon 1969; Morrison *et al.* 1975; Costa & Kooyman 1984; Davis *et al*. 1988; Riedman & Estes 1990; Yeates *et al*. 2007; Estes 2015). The sea otter's exclusive reliance on fur promoted the evolution of their luxuriant pelt (Estes 2015), making it a target to humans. Sea otters were hunted by indigenous peoples of the North Pacific prior to European contact, but it was the maritime fur trade commencing after 1741 that drove the species to the brink of extinction (Kenyon 1969). By 1911, the world population of sea otters numbered fewer than 2,000 animals scattered amongst 13 remnant colonies (Kenyon 1969; Bodkin *et al*. 1999; Bodkin 2003). As harvested sea otter populations became either reduced to unprofitable densities or locally extinct, the International Fur Seal Treaty applied a clause in 1911 to protect the remaining surviving colonies from further hunting (Lensink 1960; Kenyon 1969; Bodkin *et al*. 1999; Bodkin 2015; VanBlaricom 2015). However, efforts to restore sea otter populations began only in 1951, when some individuals were translocated from one population to another, along the Pacific coast of North America (Kenyon 1969; Jameson *et al.* 1982). Early translocations were largely unsuccessful due to the lack of knowledge on basic sea otters' biology (Bodkin 2015). Nonetheless, today, about 35% of the global sea otter abundance can be attributed to the translocations made in North America (Doroff *et al*. 2003; Bodkin 2015). Despite some fluctuations in their abundance, sea otter populations have been slowly recovering, and it is estimated that 122,875 sea otters exist today (Doroff *et al*. 2003; Bodkin 2015). However, this does not mean that the sea otter world population is out of danger (Doroff & Burdin 2015).

Contemporary issues have either prevented sea otter populations from thriving or have caused population declines throughout much of the species' range (Doroff & Burdin 2015). In the United States, two subspecies of sea otters are listed as threatened under the Endangered Species Act (ESA) due to rapid population declines in southwest Alaska, and slow growth and vulnerability to anthropogenic factors of a small subpopulation in California (Doroff & Burdin 2015). Some of these issues include, but are not limited to, environmental contamination, predation, disease events, poor genetic

diversity, habitat loss and disturbance, food limitation, competition and human take (legal, illegal, or accidental) (Ballachey & Bodkin 2015).

Anthropogenic activities' impact on wildlife is of major concern throughout the globe, and this is not different for sea otters. Oil spills are a significant threat to sea otters (Bodkin *et al*. 2002; Ballachey & Bodkin 2015). They destroy the water-repellent nature of the fur, resulting in hypothermia and death of the animal (Costa & Kooyman 1982; Williams *et al*. 1988; Estes 1991; Williams & Davis 1995). Once contaminated, the sea otter grooms itself obsessively, and stops feeding, resting and caring for pups (Ralls & Siniff 1990). Moreover, as it grooms, the sea otter ingests oil, and inhales toxic fumes, which damages internal organs (Estes 1991; Williams & Davis 1995). Other environment-related issues include direct or indirect ingestion of plastic debris and algal toxins through bottom-up effects on sea otter's prey base (Van Dolah 2000; Cole *et al*. 2011; Ballachey & Bodkin 2015). Various diseases have been documented in sea otters, many of which are known to have anthropogenic causes (review in Murray 2015), however, there is little evidence to date for consequences at a population level (Ballachey & Bodkin 2015), excluding in California, where parasites and infectious disease explains 40% of sea otters' deaths (Thomas & Cole 1996; Estes *et al*. 2003).

The recent decline of sea otters in the North Pacific is still unknown, however, it is largely believed to be due to predation by orcas (*Orcinus orca*) (Estes *et al.* 1998; Hatfield *et al*. 1998; Doroff *et al*. 2003; Gerber *et al*. 2004; Williams *et al.* 2004; Estes *et al*. 2005; Vos *et al*. 2006; Ballachey & Bodkin 2015). Other occasional sea otter predators include bald eagles (*Haliaeetus leucocephalus*) (Sherrod *et al*. 1975; Riedman & Estes 1990), white sharks (*Carcharodon carcharias*) (Ames & Morejohn 1980; Klimley 1985; Estes *et al*. 2003; Kreuder *et al.* 2003; Hulbert *et al*. 2006), brown bears (*Ursus arctos*) (Riedman & Estes 1990), coyotes (*Canis latrans*) (Monnett & Rotterman 1988) and arctic foxes (*Alopex lagopus*) (Zagrebel'nyi 2004).

Genetic diversity can be lost when a population is reduced to a small size and then allowed to increase, a phenomenon known as a bottleneck. As a result of the fur trade, genetic diversity amongst sea otter populations is

significantly low (Larson *et al*. 2002). In spite of the recovery of the remnant populations and the successful translocation efforts, many sea otter populations have remained isolated, with restricted gene flow, thus limiting the exchange of genetic material between them (Bodkin *et al*. 1999; Larson *et al*. 2012; Larson *et al*. 2015). This low genetic diversity increases the risk of extinction from stochastic events, and if a catastrophic oil spill were to occur, as it did in Alaska during the 1989 *Exxon Valdez* oil spill, and substantially reduce sea otter population, it is unlikely that recovery would be rapid (Bodkin *et al*. 2002).

Currently, the only legal human take of sea otters is in Alaska, and this is only for Alaska Natives for subsistence purposes, including the creation of qualified handicrafts, under exemption of the US Marine Mammal Protection Act of 1972 (Ballachey & Bodkin 2015; VanBlaricom 2015). However, this harvest is largely unregulated, and has the potential to reduce sea otter abundance, particularly on local scales (Bodkin & Ballachey 2010). Illegal harvest of sea otters (by non-native hunters in Alaska, and all hunting outside of Alaska) may also occur throughout the range (Lensink 1960; Ballachey & Bodkin 2015).

Conflicts between sea otters and coastal fisheries are well recognized (Ballachey & Bodkin 2015; Carswell *et al*. 2015). In the absence of sea otters throughout most of their range in the 20th century, their prey populations, such as clams, crabs, urchins, and abalones, expanded both numerically and in size (Ballachey & Bodkin 2015). In response, humans developed commercial fisheries for these resources, based on shellfish populations that were largely released from predation (Bodkin *et al*. 2004; Ballachey & Bodkin 2015). As sea otter populations expanded their range following conservation measures, they eventually came into direct competition with humans over these fisheries (Carswell *et al*. 2015; Nichol 2015). Currently, especially in southeast Alaska, many view sea otters as “vermin” that should be subjected to predator control (Carswell *et al.* 2015). However, as numerous ecological studies have shown, top predators, including marine mammals such as sea otters, provide

numerous large-scale benefits through trophic interactions (Bowen 1997; Terborgh & Estes 2010; Estes *et al*. 2011; Carswell *et al.* 2015).

1.1.2 Sea otter role in ecosystems

The long-standing debate surrounding ecological interactions between marine mammals and fisheries is rooted in the belief that marine mammals can have significant effects on prey populations of commercial interest to humans, and that in turn fisheries may impact marine mammals (Bowen 1997). Understanding the role of marine mammals in ecosystems is important, because it provides a context within which to evaluate the potential impact of their predation on prey populations and community structure; the impact of variation in prey populations by human harvesting; and the impact of environmental change on the dynamics of marine mammals (Bowen 1997). The role of sea otters in structuring nearshore communities is well documented (Estes & Palmisano 1974; Simenstad *et al*. 1978; Estes & Duggins 1995; Bowen 1997; Kvitek *et al*. 1998; Watson & Estes 2011; Estes 2015).

A keystone species is one that has an effect on community structure greater than would be expected, taking into account its abundance (Paine 1969; Power *et al*. 1996). Sea otters are a prime example of such a species because of the significant ecological effects they exert onto nearshore marine communities at rocky substrates, and their prey's life history, through top-down trophic cascades (Estes & Palmisano 1974). Sea otters are generalist predators, foraging mainly on sessile or slow moving benthic invertebrates, such as clams and crabs, but most importantly, sea urchins (Kenyon 1969; Riedman & Estes 1990; Estes 2015). In their turn, sea urchins graze extensively, and destructively, on *kelp* – brown algae of the order Laminariales, a major component of these rocky nearshore environments – forming "urchin barrens" (Estes & Palmisano 1974; Dayton 1975; Simenstad *et al*. 1978; Dayton 1985; Estes *et al.* 2004; Stewart & Konar 2012). These kelp forests are highly productive, and provide food and habitat for invertebrates and fish, which in turn support higher trophic levels, such as predatory fish, birds, and mammals (Mann 1973; Simenstad *et al*. 1978; Irons *et al*. 1986; Bodkin 1988; Duggins *et al*. 1989). For instances, the rock greenling (*Hexagrammos lagocephalus*), a common fish of kelp forests in the Aleutian Islands, is an order of magnitude more abundant in kelp forests than in urchin barrens (Reisewitz

et al. 2005). The indirect effects of sea otter predation also influence the behavior and foraging ecology of other coastal marine wildlife, such as, gulls and bald eagles (Irons *et al*. 1986; Anthony *et al.* 2008). Kelp forests also provide ecosystem services. The surface tension exerted by kelp on the water column attenuates waves and coastal currents, which in turn promotes sediment deposition, therefore reducing coastal erosion (Jackson 1984, 1997). Furthermore, kelp forests are more productive than sea urchin barrens, fixing an estimated three to four times more inorganic carbon per unit area through photosynthesis, which increases growth rates and population sizes of various consumer species (Duggins *et al.* 1989; Estes 1996; Estes *et al*. 2004; Wilmers *et al.* 2012).

In sum, when sea otters are present in a habitat, kelp forests are allowed to develop, since sea otter predation on sea urchins reduces kelp grazing, and hence, the community becomes more bio-rich and diverse (Estes & Palmisano 1974; Estes *et al*., 1978; Estes & Duggins 1995; Bowen 1997). Top-down effects of sea otters have been documented in kelp-dominated habitats and intertidal zones, such as, rocky coastal reef communities, as well as soft-sediment habitat communities (Estes & Palmisano 1974; Kvitek & Oliver 1988, 1992; VanBlaricom 1988; Estes & Duggins 1995; Estes *et al*. 1998).

Although the economic costs of sea otters are mostly well understood, there has been little effort to identify the economic benefits of sea otters (Steneck *et al*. 2002). Loomis (2006) concluded the benefits of conserving sea otter population in California will more than compensate for the estimated loss to commercial fishing. For instance, by increasing kelp bed habitat on the outer coast, and therefore supporting a greater abundance of fish and invertebrates, sea otters may benefit recreational and commercial fisheries for species, such as rockfish and lingcod, contributing significantly to the productivity of offshore habitats (Gerber & VanBlaricom 1998; Harrold *et al*. 1998; Steneck *et al.* 2002). Moreover, the marine eco-tourism industry has the potential to support a substantial number of jobs and income, and so should benefit from the recovery of the sea otter population (Steneck *et al*. 2002; Loomis 2006). Understanding sea otter's prey choices in critical places, such as southeast

Alaska where these fisheries conflicts are effervescing today, is crucial for the management of both sea otter's conservation and fisheries' economics.

1.2 Research theme

1.2.1 Foraging theory: concepts and emergent questions

Applied studies of animal behavior have played a vital role in species' conservation, mainly because knowledge on how animals behave in different environments is often necessary to inform management decisions (Tinker 2015). Foraging behavior, an organism's strategy for the acquisition of energy and nutrients, is tightly linked to survival and reproduction (Kramer 2001). Studies on foraging behavior and diet choices can provide important insights into the role of prey resources in regulating population abundance at a particular location (Tinker 2015).

Foraging theory proposes that the nutritional driver of prey choice and foraging in carnivores is energy gain (Charnov 1976; Pike *et al.* 1977; Stephens & Krebs 1986; Whelan & Schmidt 2007). In fact, as assumed in the studies by Antonelis *et al*. (1981) and Ostfeld (1982), sea otters select prey with higher caloric-intake to compensate their foraging effort ratios. In contrast, recent research suggests that carnivores select prey that provides a diet with a specific balance of macronutrients (fat, protein, carbohydrates), rather than the highest energy content (Mayntz *et al*. 2009; Hewson-Hughes *et al*. 2011, 2012, 2013). However, these studies have been undertaken only in few carnivore species, namely, invertebrate species (beetles and spiders) (Mayntz *et al*. 2005; Jensen *et al*. 2012), few vertebrates (fish and birds) (Yamamoto *et al*. 2001; Rubio *et al*. 2003, 2009; Tait *et al*. 2014; Machovsky-Capuska *et al*. 2016b), and domesticated terrestrial mammals (mink, cats, and dogs) (Mayntz *et al*. 2009; Hewson-Hughes *et al*. 2011, 2012, 2013; Plantinga *et al*. 2011; Jensen *et al.* 2014; review in Kohl *et al.* 2015). Thus, it remains to be determined whether wild mammalian carnivores feed selectively according to macronutrient balance, how does this applies to marine mammals, and how nutritionally variable the foods of predators are in the wild (Kohl *et al*. 2015; Machovsky-Capuska *et al*. 2016a). Answers to such questions not only will have significant implications for managing predator populations and the ecological communities of which they are a part, but will also add important

information on predator biology that has been neglected so far (Raubenheimer *et al.* 2009; Simpson *et al*. 2010; Kohl *et al*. 2015).

1.2.2 Sea otter feeding behavior, with emphasis in southeast Alaska

Due to a number of aspects of their behavior and biology, sea otters are uniquely suited to studies of foraging behavior and diet. Sea otters bring all captured prey to the surface to handle and consume, and they do this while lying on their backs (Estes *et al*. 1981, Kvitek *et al*. 1993, Doroff & DeGange 1994; Tinker 2015). Further, their foraging success rates may reach 90% (Estes *et al*. 1981, Kvitek *et al*. 1993, Doroff & DeGange 1994; Wolt *et al.* 2012; Tinker 2015). This behavior, in combination with their nearshore distribution and short diving depths of 100 meters or less (Riedman & Estes 1990; Bodkin *et al*. 2004), makes them ideal subjects for shore and boat-based observational studies of feeding behavior.

In response to their high metabolic rate, free-ranging sea otters need to consume the equivalent of more than 20% of their body weight in prey per day (Costa 1978; Costa 1982). The sea otter is a known opportunistic feeder and generalist predator throughout its range, preying on at least 150 different species, mostly benthic invertebrates, such as clams, snails, chitons, limpets, octopi, crustaceans, starfish, sea urchins, sand dollars, anemones, polychaete worms, echiuriods, tunicates, sea cucumbers, fish and kelp (Kvitek *et al*. 1991), but individually they may specialize on just a few prey items (Kenyon 1969; VanBlaricom 1988; Riedman & Estes 1990; Estes & Bodkin 2002).

The predominately mixed-sediment habitats of southeast Alaska support populations of clams that are the primary prey of sea otters here, although sea urchins and mussels can also be important (Calkins 1978; Kvitek & Oliver 1992; Kvitek *et al*. 1993; Doroff & Bodkin 1994; Doroff & DeGange 1994; Wolt *et al*. 2012). Presumably, in the absence of sea otters, these populations of macroinvertebrates increased, and lucrative fisheries developed to exploit the accumulated abundance of shellfish in southeast Alaska (Carswell *et al*. 2015). However, as sea otters continued to increase in number and expanding their range during the 2000s, fishermen became increasingly agitated about competition with sea otters for shellfish (Carswell *et al.* 2015). What is more, it is assumed that a recovering sea otter population is impacting negatively commercial fished species, because they deplete sea cucumbers, red sea

urchin, geoduck clams, and Dungeness crab in southeast Alaska below levels needed to sustain a fishery, causing seriously conflicts between fisheries and sea otter conservation (Davidson *et al*. 1993; Larson *et al*. 2013; Carswell *et al.* 2015; Hoyt 2015).

The degree of sea otter prey specialization primarily may depend on the abundance of prey, and, if the habitat is food-rich, specialization may not occur (Riedman & Estes 1990; Laidre & Jameson 2006; Tinker *et al*. 2008; Wolt *et al*. 2012). Studies conducted across the range of sea otters have shown that when the abundance of sea otters' preferred prey is reduced, they turn to other available foods, and so their diet increases in diversity, but decreases in energy intake rates over time (Estes *et al*. 1981; Ostfield 1982; Tinker *et al.* 2012; Weitzman 2013). It is not clear, however, if sea otters select diets composed of specific ratios of macronutrients when presented with different prey choices.

1.3 Study aims, objectives, and hypotheses

Understanding how sea otters choose prey items is of crucial importance, because of the different areas it affects. The goals of this research are to: 1) update and advance the state of knowledge on the biology and prey choice of sea otters in Sitka Sound, southeast Alaska; 2) advance knowledge of carnivore foraging ecology by determining if and how a top marine predator selects prey according to nutritional content; and 3) apply results towards informing conservation and management decisions regarding fisheries and sea otters.

These goals will be achieved through the specific objectives to: 1) describe sea otter's diet in Sitka Sound, southeast Alaska; 2) describe the nutritional value of sea otters' prey items; 3) compare differences in prey choice according to sex; and 4) evaluate and compare prey's nutritional value with sea otter's prey choices.

I hypothesize that 1) there are significant differences in prey choice by sea otters; 2) prey choice varies by sex; and 3) there are significant differences in preferred prey's nutritional content.

2. MATERIAL AND METHODS

2.1 Study area

This study was carried out in Sitka Sound (56°58'13.19"N, 135°29'16.19"W), located in southeast Alaska (Figure 2). This is a water body surrounded by the boundaries of the Tongass National Forest, a temperate rainforest that is exposed to the North Pacific Ocean, and is the largest forest in the United States. Sitka sound's coastal habitat is predominantly of mixed-sediments, with sandy beaches and rocky intertidal zones, rich in underwater kelp forests. This area provides habitat to a number of wildlife, including, marine invertebrates, fish, coastal brown bears, deer, marine birds, eagles, cetaceans, pinnipeds and sea otters. Due to the intensive fur exploitation between 1741 and 1911, this area was eventually free of sea otters, until conservation measures were taken (Bancroft 1959; Kenyon 1969). Translocations of individuals to restore sea otter Alaskan southeast populations were made from Amchitka Island in southwest Alaska, and Prince William Sound in southcentral Alaska, to scattered regions of southeast Alaska (Jameson *et al*. 1982; Simon-Jackson & Hodges 1986). By the early 1970's, translocated sea otters were reported to have established reproducing populations in southeast Alaska, accounting for 25,712 estimated individuals, as of 2012 (Jameson *et al.* 1982; Simon-Jackson & Hodges 1986; Esslinger & Bodkin 2009; USFWS 2013; Carswell *et al*. 2015). As a result, sea otters spread to Sitka Sound in the early 2000's (Estes 2016), and this area has had a reliable presence of sea otters for the past decade, with vessel tours running all summer for the viewing of wildlife, mainly sea otters.

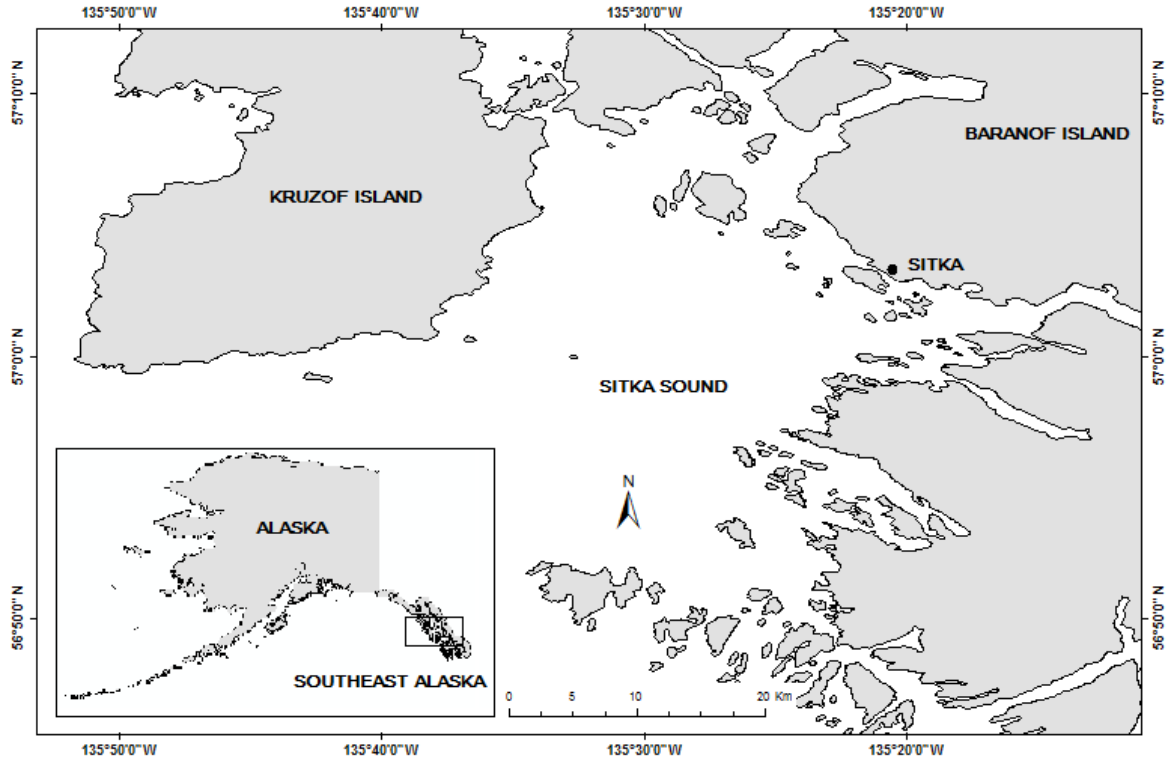

Fig. 2 Study area. Sitka Sound is located in southeast Alaska, surrounded by Kruzof island, Baranof island, and open to the North Pacific Ocean.

2.2 Field procedures

2.2.1 Sea otter's behavioral observations and prey identification

In order to have a better understanding of the main prey items that the sea otter consume in Sitka Sound, boat-based observations were conducted during the months of May, June, July and August of 2016, from catamarans ran by a wildlife tour company, Allen Marine Tours, varying in length from 48 to 72 foot, and powered by 1000 to 2400-hp engines (Figure 3). Allen Marine Tours usually ran tours twice a day, with random routes when looking for wildlife (i.e., whales, sea lions, harbor seals, coastal bears, coastal deer, marine birds, bald eagles, and sea otters). When a group of sea otters - *raft* - was spotted, the vessel lingered there for about 10 minutes before departing to another location to look for more wildlife. Sea otters are habituated to vessel tours and usually carried out with their activities, nonetheless, vessels kept at >10 meters' distance from the sea otters. However, feeding sea otters usually distanced themselves about >20 meters from the boats. When the vessel was on route, some scattered single sea otters could also be spotted, however the boat usually did not stop for the viewing of these single sea otters.

Fig. 3 Wildlife watching boat tour in Sitka, Alaska; platform of opportunity for the observation of sea otters. Photo by Bárbara Cartagena S. Matos

Foraging observational data were collected opportunistically. Whenever sea otters were sighted, data collection began. Sea otter's behavior was scanned with the help of 10x42 binoculars, and individuals exhibiting foraging behavior, with good viewing conditions, were targeted for observation and photographed through *ad libitum* sampling (Altmann 1974) until they were out of sight. A sea otter was considered to be foraging when it was observed repeatedly diving underwater and returning to the surface to either consume prey or breathe before diving again (Bodkin 2011). Photographic pictures of feeding sea otters were taken with digital camera Canon PowerShot SX40 HS 24-840mm zoom lens, for posterior analysis and prey identification. Other data were also collected in the end of each sighting, such as, weather conditions, including percentage of cloud cover, sea state (according to Douglas scale), wind state (according to Beaufort scale), precipitation (0: no rain; 1: light rain; 2: heavy rain), and visibility (on a scale from 0-9, with 0 representing very poor visibility and 9 perfect visibility); date; time; location recorded with GPS (Garmin, GPSMAP 78); estimated distance to sea otters; number of individuals in a raft; indication of male or female raft (through presence or absence of pups); number of pups; and, if possible on site, prey identification, quantity and size.

At the end of each sampling day, data was input in excel data sheet, and sea otter photos were analyzed. Whenever possible, sex of the feeding sea otters was recorded. Sex was identified by the presence or absence of penile bulge and pup (Bodkin 2011). Prey species, number and size were recorded. Prey size was estimated using the sea otters' forepaw width as a reference, with an average width of about 5 cm (approximately 1.96 inches) (Bodkin 2011). Prey items were identified to the lowest possible taxon, and were classified as "unknown" when no identification could be made.

2.2.2 Sea otter's prey capture

In order to have a better understanding of the nutritional content of the main prey items that the sea otters consume in Sitka Sound, a permit to capture sea otter's prey samples was obtained through the Department of Fish and Game of the State of Alaska. During two weeks of July 2016 and another two weeks of August 2016, research biologists of the Sitka Sound Science Center scuba dove and hand-captured some of the possible main prey items in arbitrary areas of Sitka Sound (according to Bodkin *et al.* 2001; Delorme, unpublished data), namely, two (2) red sea urchin (*Strongylocentrotus franciscanus*); one (1) green sea urchin (*Strongylocentrotus droebachiensis*); one (1) California sea cucumber (*Parastichepus californicus*); one (1) scallop (*Chlamys hastata*); one (1) Northern kelp crab (*Pugettia producta*); one (1) abalone (*Haliotis kamtschatkana*); one (1) Northwest ugly clam (*Entodesma navicular*); four (4) butter clam (*Saxidomus giganteus*); and four (4) steamer clam (*Protothaca staminea*) (Figure 4). These prey items were euthanized on site, frozen and sent to the Alaska Fisheries Science Center's Auke Bay Laboratories (ABL), of the National Oceanic and Atmospheric Administration (NOAA), for further analysis.

Fig. 4 Research biologist scuba diving and capturing sea otter's main prey species (e.g., sea urchin). Photo by Lauren Bell

2.3 Laboratory analysis

2.3.1 Prey's nutritional content

The Alaska Fisheries Science Center's Auke Bay Laboratories (ABL), of the National Oceanic and Atmospheric Administration (NOAA), offered to analyze up to 16 prey items to determine the nutritional composition of sea otter main prey. During September, October and November 2016, the captured prey samples were analyzed for percentage in lipids (fat content), and calories (energy density).

Percent lipid composition was determined using a sulfo-phospho-vanillin (SPV) colorimetric analysis adapted or use in a 96-well plate format (Handel 1985). In brief, each sample was weighed to the microgram in a tared glass vial. 2 mL of 2:1 chloroform-methanol (w/v) was added to each sample and the samples were sonicated for 30 minutes. Supernatant was transferred to a glass 96-well plate and evaporated to dryness at 100 °C. 20 µL of concentrated sulfuric acid was added to each well and the 96-well plate was heated at 100 °C for 10 minutes. The 96-well plate was allowed to cool to room temperature before 280 µL of SPV reagent (7.9 mM vanillin, 11.84 M) was added to each well. The 96-well plate was allowed to incubate at room temperature with gentle shaking for 30 minutes. The absorbance at 490 nm of each well was recorded. The amount of lipid was calculated by comparison to a calibration curve made using diluted Mehaden oil. An in-house Pollock standard was used for quality insurance during each assay. In order to determine the amount of calories (energy density) of the prey items, a subsample of approximately 15 mg of powder was compressed into a pellet for combustion in a Parr 1425 micro-bomb calorimeter. Whole body energy density (kJ/g DW) was determined using methods described previously (Orson & Fergusson 2014). Moisture content were measured gravimetrically using a LECO Thermogravimetric Analyzer (TGA) 601. A temperature of 135 °C was used to determine moisture content.

2.4 Data analysis

For purposes of data analysis, prey species observed in the field were collapsed into prey classes, namely clams, scallops, sea cucumbers, sea urchins, crabs, and sea stars. Frequencies of occurrence of the different prey classes observed in the field were calculated for the overall diet of sea otters, and male versus female sea otters. Chi-square tests (X^2) were used to test for significant differences between prey classes' frequency of consumption, and to test if consumption of different prey classes varied significantly between male and female sea otters. Likelihood ratio was used for the latter analysis. Average and median values on lipids and calories (energy density) of the prey items analyzed in the lab were calculated, in order to fit them into the same prey classes, and to learn the overall macronutrient dietary composition of sea otters. These values were also calculated for both sea otter' sexes. The Shapiro-Wilk test (*W*) was used to test for normality of data. Then, the Kruskal-Wallis test (*H*) was used to look for significant differences in terms of content of lipids and calories, between prey classes. Afterwards, a Mann-Whitney test (*U*) was used to test for differences in frequency of lipids and calories in sea otter's prey, between males and females. All data were analyzed using the statistical computer program *SPSS* version 23 (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 23.0. Armonk, NY: IBM Corp), and the significance level was set as $p<0.05$.

Because no sea stars were collected during scuba dives, nor any abalone was seen being consumed by sea otters during field observations, these two prey items were not considered for the latter analysis. Each identifiable prey item was considered an independent sample and the smallest sampling unit for statistical analysis. Moreover, only identifiable prey items of sea otters whose sex was perceptible were considered for analysis.

3. RESULTS

Throughout May-August 2016, 95 field trips were conducted, totaling 283 hours and 45 minutes of fieldwork, of which 23 hours corresponded to direct observation of sea otters (see Appendix 2). During this sampling period, 246 sightings of either rafts or single sea otters, were observed. During these sightings, 68 sea otter's prey items were detected, of which 41 were identifiable, however, of these, 35 (*n*) were consumed by sea otters whose sex was possible to classify.

The 35 individual prey items sighted in the field included clams (*n*=24), which had the highest frequency of occurrence on the diet of sea otters (68,6%), followed by sea urchins (*n*=5, *F*=14,3%), scallops (*n=2*, *F*=5,7%), sea cucumbers (*n*=2, *F*=5,7%), crabs (*n*=1, *F*=2,9%) and sea stars (*n*=1, *F*=2,9%) (Table 1). Consumption by sea otters proved to be significantly different between prey items (χ^2= 69.743, df= 5, p= 0.000).

Clams were more frequently consumed by male sea otters (*n*=16, *F*=67%) than females (*n*=8, *F*=33%), whilst sea urchins were more frequently consumed by females (*n*=3, *F*=60%), than males (*n*=2, *F*=40%). Sea cucumbers were equally consumed by males (*n*=1, *F*=50%) and females (*n*=1, *F*=50%). Scallops, sea stars, and crabs, were never seen being consumed by female sea otters (Table 1). Consumption of different prey items between male and female sea otters was not significantly different (χ^2, likelihood ratio = 4.948, df= 5, p= 0.422).

Table 1. Frequency of occurrence of the prey items consumed by male and female sea otters, in Sitka Sound (*n*: sample size).

Prey items	Total	Female sea otters	*n*	Male sea otters	*n*
Clam	68,6%	33,3%	8	66,7%	16
Scallop	5,7%	0%	0	100%	2
Sea cucumber	5,7%	50%	1	50%	1
Sea urchin	14,3%	60%	3	40%	2
Crab	2,9%	0%	0	100%	1
Sea star	2,9%	0%	0	100%	1

In the lab, 16 prey items were analyzed for their content on lipids, and calories. Their average values were calculated and fit into five main prey classes (Table 2). The Shapiro-Wilk (*W*) normality test revealed that this data does not follow a normal distribution for lipids (W=0.684, p=0.000, n=34), nor for calories (W=0.732, p=0.000, n=34). The Kruskal-Wallis test (H) revealed a statistically significant difference in lipid percentage (H=33.00, df=4, p=0.000), and energy density (H=33.00, df=4, p=0.000), across the five different prey classes.

Table 2. Prey items analyzed in the lab, their content on lipids and calories, and average and median values within specimens, and prey class, in Sitka Sound.

Prey class	Number of prey items	Prey		Lipids[a] (%)	Average of prey species	Average of prey class	Median of prey class	Calories[b] (KJ/g)	Average of prey species	Average of prey class	Median of prey class
Clams	4	Butter clam	*Saxidomus giganteus*	0.764	0.877	**0.784**	0.727	2.411	2.581	**2.217**	2.298
				1.022				3.039			
				0.703				2.214			
				1.019				2.662			
	4	Steamer clam	*Protothaca staminea*	0.481	0.442			1.313	1.703		
				0.314				1.202			
				0.244				2.002			
				0.727				2.298			
	1	Northwest ugly clam	*Entodesma navicula*	1.780	-			2.816	-		
Sea urchins	2	Red sea urchin	*Strongylocentrotus franciscanus*	0.753	1.101	**1.751**	1.448	0.697	0.788	**1.351**	0.880
				1.448				0.880			
	1	Green sea urchin	*Strongylocentrotus droebachiensis*	3.052	-			2.476	-		
Sea cucumbers	1	California sea cucumber	*Parastichepus californicus*	**0.240**	-	**-**		**1.167**	-	-	
Scallops	1	Scallop	*Chlamys hastata*	**1.639**	-	**-**		**3.357**	-	-	
Crabs	1	Northern kelp crab	*Pugettia producta*	**1.239**	-	**-**		**3.213**	-	-	
-	1	Abalone[c]	*Haliotis kamtschatkana*	1.461	-	**-**		4.035	-	-	

[a]Percentage of lipid was calculated on a wet mass basis (grams lipid / grams wet tissue * 100).
[b]Calories, or energy density, was calculated on a wet mass basis (kilojoules / grams wet tissue).
[c]Abalone was not included in the final data analysis, since it was not seen eaten by the sea otters.

Average values on lipids and calories of the prey classes analyzed were calculated overall, and for both sea otter' sexes (Table 3). The Shapiro-Wilk (*W*) normality test revealed that these data do not follow a normal distribution for males (lipids: W=0.673, p<0.000, n=22; calories: W=0.727, p<0.000, n=22), nor females (lipids: W=0.717, p<0.001, n=12; calories: W=0.646, p<0.000, n=12). The Mann-Whitney (*U*) test revealed no significant difference in the lipid levels of males (Md=0.784, n=22), and females (Md=0.784, n=12), U=128.500, z= -0.157, p= 0.875. Similarly, the Mann-Whitney (*U*) test also did not reveal significant difference in the energy density levels of males (Md=2.217, n=22), and females (Md=2.217, n=12), U=94.500, z= -1.682, p= 0.092.

Table 3. Average values of lipids and calories of the consumed prey overall, and by male and female sea otters.

	Lipids (%)	**Calories (KJ/g)**
Male sea otters	0.945	2.239
Female sea otters	0.980	1.913
Overall	0.957	2.214

4. DISCUSSION

This four-month study aimed to investigate the foraging ecology of sea otters residing in Sitka Sound, located in southeast Alaska. More specifically, what are the most consumed prey species in this area; if predation is driven in accordance to prey's nutritional content; and if this varies by sex.

4.1 Prey choice and nutritional content

As predicted by optimal foraging theory, sea otters should prefer food species of high rank and replace depleted dietary items with those of next highest rank (Ostfeld 1982; Pyke 1984). This selection of prey is thought to be made according to prey's energy intake, presumably to meet sea otters' high metabolic requirements (Antonelis *et al*. 1981; Ostfeld 1982; Garshelis 1983; Pyke 1984). Studies suggest that sea urchins are often the first prey species targeted by sea otters after colonization, being heavily preyed upon initially, but eventually disappearing from their diet (Ostfeld 1982; Hoyt 2015). Once preferred prey is reduced, the sea otters' diet diversifies to include clams, sea cucumbers and small crabs, with the most diverse prey composition being found at sites occupied longest (Ostfeld 1982; Riedman & Estes 1990; Kvitek & Oliver 1992; Laidre & Jameson 2006; Tinker *et al*. 2008; Lee *et al*. 2010; Wolt *et al*. 2012; Hoyt 2015). Thus, their diet increases in diversity, but decreases in energy intake rates over time (Estes *et al*. 1981; Ostfeld 1982; Tinker *et al*. 2012; Weitzman 2013). However, recent research suggests that carnivores select prey that provides a diet with a specific balance of macronutrients (fat, protein, carbohydrates), rather than the highest energy content (Mayntz *et al*. 2009; Hewson-Hughes *et al*. 2011, 2012, 2013). Such research has never been studied in a wild carnivore marine mammal (Kohn *et al*. 2015).

In this study, sea otters showed significant differences in prey choice, as expected, consuming more clam than other prey species. Indeed, clams represent an important component of sea otters' diet across Alaska, as seen in previous studies (Calkins 1978; Garshelis *et al.* 1986; Kvitek 1990; Kvitek

& Oliver 1992; Kvitek *et al*. 1993; Doroff & Bodkin 1994; Doroff & DeGange 1994; Bodkin *et al*. 2006; Wolt *et al*. 2012). In different locations in southeast Alaska, clams were consistently larger and more abundant than sea urchins, and continued to serve as a major prey base for sea otters in Alaska long after sea urchins were nearly eliminated, even though sea otters greatly reduced both clam and sea urchin populations (Kvitek & Oliver 1992; Kvitek *et al*. 1993). As such, according to optimal foraging theory, sea urchins and clams should be the biggest source of energy intake of all main prey species for sea otters here. However, in this study, the results revealed a significant diversity in content of fat (lipids) and energy density (calories) between sea otter prey specimens, rather than a clear ranking of preferred species according to highest energy densities or lipid content per prey. Abalone ranked first on content of energy density, however this prey was never seen being consumed by sea otters in this study, as also reported by Hoyt (2015), in several regions of southeast Alaska. On the other hand, the sea urchin prey class, the second most consumed species in this study, recorded the highest lipid content, as seen in Oftedal *et al*. (2007), though it was one of the lowest ranked, regarding energy density. Even though clams had the highest frequency of consumption in this study, they did not rank the highest in energy density or lipid content. Nevertheless, the results presented here should be interpreted with caution, since sample size is very small.

The results in this study showed little evidence of prey specialization among sex categories, as also seen in other areas of southeast (Kvitek *et al*. 1993), and southcentral Alaska (Wolt *et al.* 2012). Although a high degree of prey specialization was not apparent, clams were more frequently consumed by male sea otters than females, whilst sea urchins were more frequently consumed by females than males. Sea cucumbers were equally consumed by males and females. Scallops, sea stars, and crabs, were never seen being consumed by female sea otters. There was also no apparent difference in the nutritional content of prey between male and female sea otters, however, a difference in prey's nutritional content might be possible to observe between females with pups, and females without pups and males, since females might

obtain higher energy prey in order to share it with their descendants (VanBlaricom 1988; Lee *et al*. 2010). In this study, data on the foraging behavior of females with pups was not possible to collect.

Nonetheless, clams appear to be the most important prey for sea otters, able to sustain a population for much longer periods, even though they have relatively low energy per gram of tissue, and are more energetically demanding to capture than other species (Estes *et al*. 1981; Garshelis *et al*. 1986; Kvitek & Oliver 1992; Kvitek *et al.* 1993; Estes & Bodkin 2002; Oftedal *et al*. 2007; Walker *et al*. 2008; Wolt *et al*. 2012; this study). Although variation in prey species composition among sites may also reflect differences in prey availability among those sites, rather than differences in prey selection by sea otters (Bodkin *et al.* 2006), the results presented here, and the fact that this prey choice in this study is similar to other areas in Alaska, may suggest some form of prey selection occurring that may be independent of prey abundance or energy intake alone. Further and more extensive research is needed on sea otter's diet.

4.2 Limitations and future research

In this study it was possible to sight several rafts of sea otters in a period of four months, however, foraging observations were much scarcer than expected. Although sea otters didn't seem to be bothered by the Tour boats, feeding individuals would normally separate from their raft and from the boat, which made prey observation more difficult. Another possible limitation to this study was difficulty in identifying prey species and its size in the field. Sea otters bring their food to the surface to handle them (Estes *et al*. 1981, Kvitek *et al*. 1993, Doroff & DeGange 1994; Tinker 2015), but several observed prey were already partially consumed, which made prey identification impossible in those cases. Male sea otters appeared to be more comfortable and curious around Tour boats, which made them easier to observe than females, leaving room for possible bias towards male sea otters, regarding feeding observations.

Even though this study does not provide data on sea otter prey abundance in Sitka Sound, prey selection in this area is similar to other areas in Alaska (Calkins 1978; Kvitek 1990; Kvitek & Oliver 1992; Kvitek *et al*. 1993; Doroff & Bodkin 1994; Doroff & DeGange 1994; Bodkin *et al.* 2006; Wolt *et al.* 2012), so there appears to be some form of prey selection occurring that may be independent of prey abundance. Nonetheless, main prey abundance data should be something to include in future studies. This study was able to determine some nutritional content in sea otter prey, and show significant differences in fat and energy density content between different prey, however, for logistical reasons, it was not possible to determine protein content of prey. In order to better assess whether wild sea otter's diet is composed of a balanced macronutrient diet, it is important to also determine proteins (Tait *et al*. 2014). Nevertheless, the work on carnivore nutrition is preliminary, and these results provide a starting point for future work.

The reintroduction of sea otters to southeast Alaska is a conservation success story (Hoyt 2015), however, communities' conflicts over the impacts sea otters are having on commercial shellfisheries in this area cannot be overlooked, as it can lead to legislation targeted at reducing sea otter

abundance (Davidson *et al*. 1993; Larson *et al*. 2013; Carswell *et al*. 2015). Sea otters are a keystone species for the nearshore Pacific Coast; absence of sea otters can lead to major changes in the local ecosystem, that will ripple on many levels of the food web, from kelp forests to commercial fisheries (Estes & Palmisano 1974; Simenstad *et al.* 1978; Estes & Duggins 1995; Bowen 1997; Kvitek *et al*. 1998; Watson & Estes 2011; Estes 2015). Rather than being targeted for extermination, sea otters should be included in the management of nearshore fisheries and harvest levels, taking into account an ecosystem perspective, including, for instances, predation rates of sea otters on shellfish abundance (Hoyt 2015). Understanding sea otter's prey choices may provide information and predictions of how fisheries may be affected as the sea otter population grows in this area, in order to help decision makers, policy makers, community members, and commercial fishermen respond accordingly.

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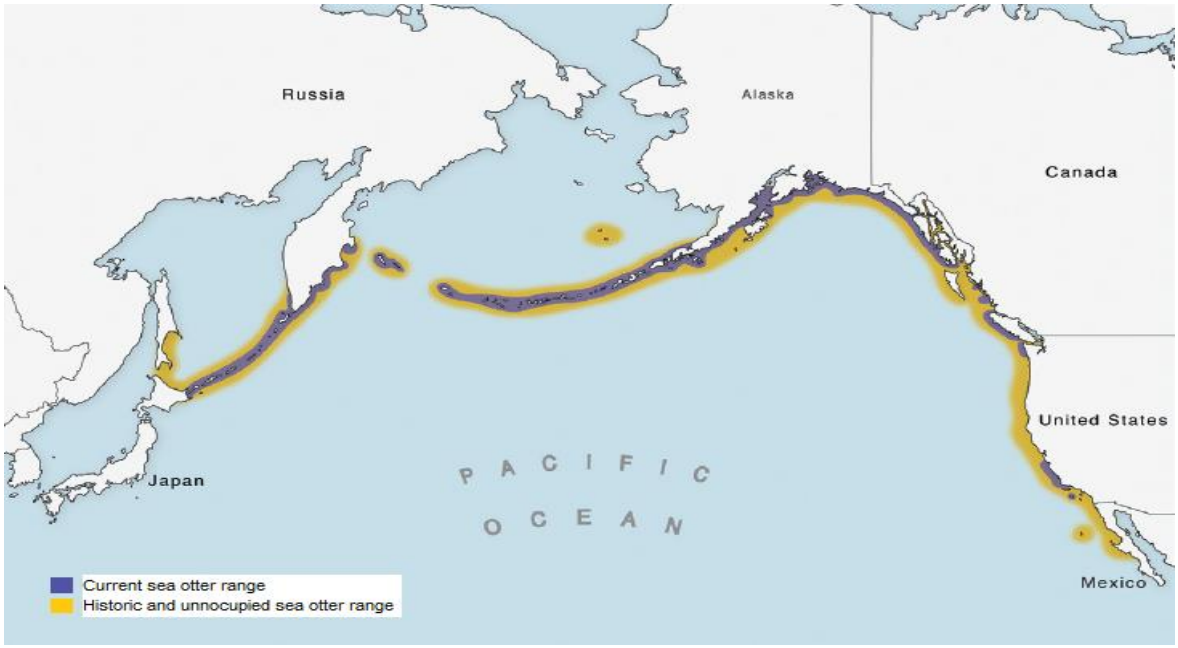
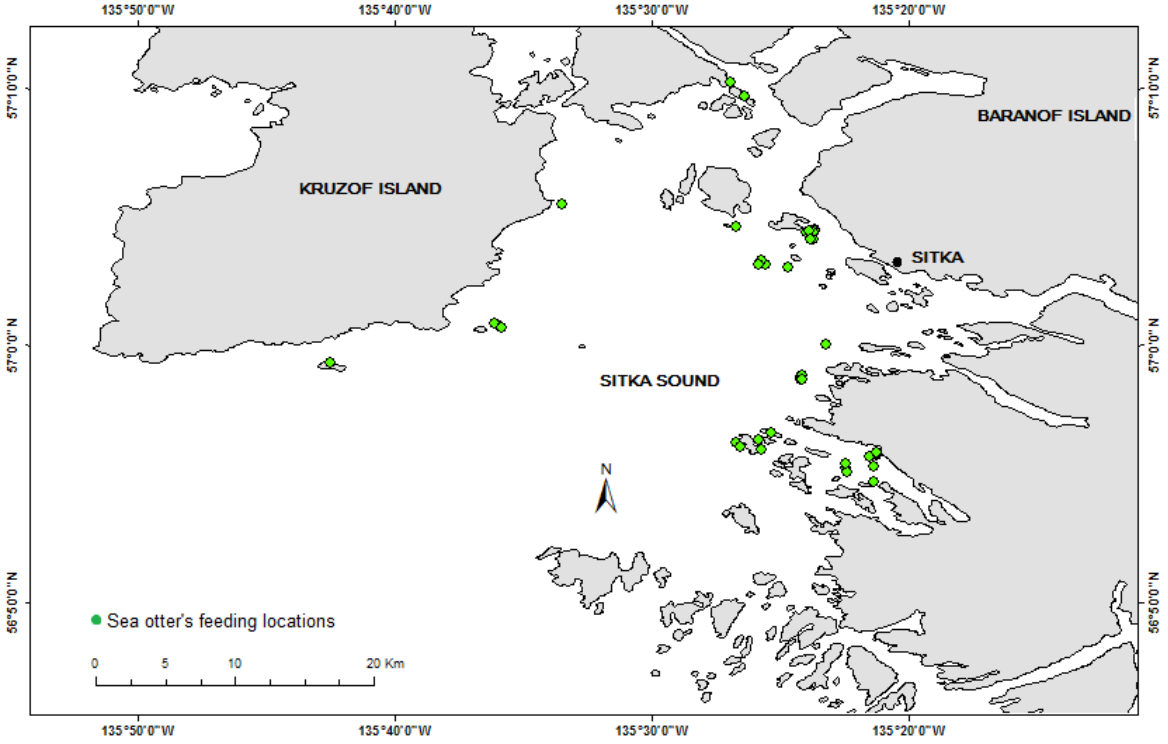
APPENDIX

APPENDIX 1



Historic (yellow) and current (purple) global range of all three subspecies of sea otters (adapted from Larson & Bodkin 2015).

APPENDIX 2



Sea otter's feeding locations in Sitka Sound, Southeast Alaska.